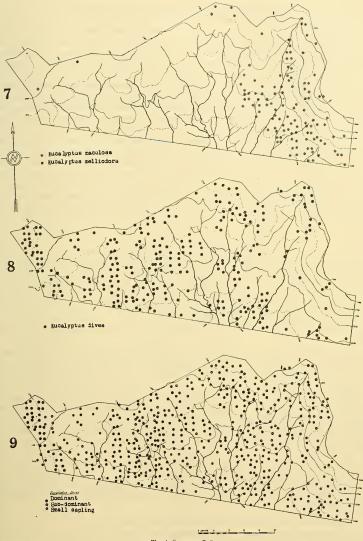


Text-figures 4-6.

which show some overlap. For the area concerned the overlap of these two species is about 15% of their total distribution, which compares with only about 1% between *E. dives* and *E. Rossii* within the same limits. While this difference needs further explanation, it will be seen at once that the amount of overlap is quite different from that of non-interbreeding species which, for example, in the case of *E. macrorrhyncha* is co-extensive with *E. maculosa* for about 75% of the area covered by the latter species.



Text-figures 7-9.

It is obvious that the extent of overlap is partly related to the habitat requirements of the species. For example, *E. Robertsoni* requiring good soil and sheltered conditions needs a habitat which is strongly contrasted with that occupied by *E. Rossii* which can survive naturally only on exposed slopes with poor rocky soil. These habitats are strongly contrasted and any intermediate zone is usually too exposed for *E. Robertsoni* or too sheltered for *E. Rossii*, their place being taken by the Renantherous species

E. macrorrhyncha. This difference is reflected in the fact that they do not overlap at all in the area and barely come into contact in one or two places. On the other hand, the requirements of E. dives and E. macrorrhyncha are much closer and at their junction there is obviously a gently grading habitat which can readily accommodate both species. In a broad view extending to the full range of these species beyond the marginal area being studied, E. dives and E. macrorrhyncha do not occur together as co-dominants in stands. E. dives is distributed at elevations above E. macrorrhyncha, so that as one proceeds higher on the Southern Tablelands the same habitat which carried E. macrorrhyncha alone or with a non-interbreeding species at the warmer northern end is found to have E. dives alone or similarly combined in the colder southern areas, as, for example, to the south of Michelago towards Cooma and Jindabyne. The rather broad overlap of the two species in the subject area, however, probably results from another cause. This is illustrated by Text-figures 8, 9, 10 and 11, showing the distribution of E. macrorrhyncha and E. dives. It will be noticed if these figures are compared, that since settlement, which has meant burning and partial clearing followed by extensive regeneration, E. dives has extended its range much more than E. macrorrhyncha. The new conditions favour E. dives, as indicated from the figures. The dominants are large, old trees which would correspond quite closely to the virgin stand. Co-dominants are mostly the early regeneration following settlement and the saplings or dominated trees are plants up to about thirty years of age. The response of various species to the new conditions resulting from settlement is quite variable; some are aggressive and spread rapidly, like E. dives, whereas others tend to remain restricted or even diminish, as, for example, E. maculosa. It is likely, therefore, that the overlap between E. dives and E. macrorrhyncha was even less than the figures indicate but, on the other hand, in the future the overlap will become still greater as E. dives extends its range in accordance with the regeneration already established and the favouring of further regeneration by present conditions. In the virgin state the zone of overlap between E. dives and E. macrorrhyncha is small and quite precise compared with present-day conditions.

This area illustrates particularly well another type of junction zone of interbreeding species.

As mentioned above, *E. Rossii* and *E. Robertsoni*, as a result of their habitat requirements, do not overlap and barely approach one another at one or two points. The intermediate habitat zone is occupied by *E. macrorrhyncha* in so far as Renantherae are concerned (Text-figs. 4 and 12).

When the survey of this area was carried out in 1938 trees distinct from either E. Robertsoni or E. Rossii but possessing some of the characters of either, were recognized in this intermediate zone. In particular, their Peppermint affinity was quite apparent, but as at that stage nothing was known of their genetic make-up, they were accordingly recorded as a new species of Eucalyptus with Peppermint affinities. The genetic constitution of these trees has been subsequently determined, and it is clear that they are E. Rossii \times E. Robertsoni hybrids. Text-figure 13 shows three features of the occurrence of these hybrids which are of interest. Firstly, they are in the intermediate habitat; secondly, there are some old trees which were present before settlement; and thirdly, the range and number of the hybrids have extended in regrowth since settlement.

CHARACTERISTICS OF SPECIES JUNCTIONS.

From similar field studies it is found that in the area where two interbreeding species of *Eucalyptus* meet there is usually a zone of hybrids between the two species to a greater or lesser degree. The extent of this zone and the number of actual hybrids are affected by several things. First of all it is likely that the ease of hybridizing between all pairs of parents is not the same, and secondly, the viability of the offspring from the combinations is apparently not uniform. In addition, the type of habitat and the rapidity of change in gradation between the two habitats at times eliminate most of the space in which hybrids with growth requirements approximately between the two parents can thrive, or it may be practically non-existent, as in the case of the very sharp transition from the swampy accumulated soils ordinarily occupied by *E. stellulata* to those occupied by, say, *E. macrorrhyncha*.

A careful examination of a number of species junctions in different areas shows that old hybrid trees, which were growing before settlement, occur in many cases, even though rather sparsely, e.g., *E. pauciflora* \times *E. fastigata* at the upper limit of the *E. fastigata* is fairly frequent, and *E. gigantea* \times *E. pauciflora* is found. The same kind of thing has been observed in widely different regions, for example, between *E. melanophloia* and *E. albens* about thirty miles west of Tenterfield on the Bonshaw road; between *E. micrantha* and *E. campanulata* at the edge of the scarp about fifteen miles east of Tenterfield; between *E. sideroxylon* and *E. albens* in the vicinity of Gundagai; and *E. leucoxylon* and *E. odorata* on the Adelaide plains. As a result of this reconstruction of the conditions of hybrid occurrence in virgin stands, it is shown that in many cases the formation of hybrids has been going on for an indefinitely long time, but under virgin conditions they have been able to thrive successfully only in a small area at the junction of the two species.

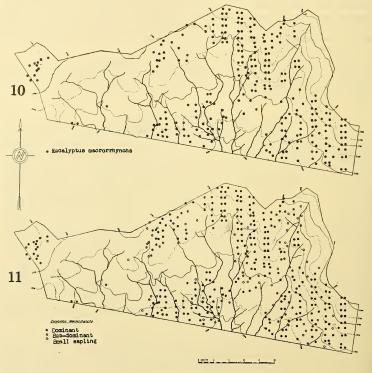
There is some evidence that in addition to the occurrence of hybrids in the junction zone there is a degree of introgression by either species, one into the other, usually present. Further study is necessary, however, to understand fully the position in this particular respect.

SPREAD OF HYBRID SWARMS.

It is not difficult to account for the extensive development of hybrid swarms between various species combinations following settlement, and it does not seem necessary to postulate an altered rate of hybridization between any given pair of species to account for the present condition. At the time of settlement a reservoir of hybrids was already present, and the result of settlement has been the upset of balance, the "hybridization of the habitat" (Anderson, 1949), which has favoured the spread of progeny derived from hybrids of one kind or another at the expense of species occupying the adjoining zones in the virgin state. It has already been mentioned in the case of E. dives that the conditions following settlement favour the regeneration of that species. This fact is clear and it can be demonstrated easily that it is associated with fire, although all the details of the process are not yet known. The result is, however, that certain hybrid combinations derived from species favoured in their growth by the new conditions are even more successful than their parents in spreading at the expense of other species, and this is expressed in mountain areas in the Australian Capital Territory by the advance of certain Renantherous species at the expense of some of the Macrantherae. Moreover, this often makes available to Renantherous species a site which was not well, or even at all, occupied by either of them in the virgin state. In such circumstances hybrids often thrive better than either of the invading parent species.

A good example of this is provided by the area in the vicinity of Lees Springs, A.C.T. Approaching the top of the range there is a gently grading broad gully which gradually becomes less sheltered and, while at first carrying a stand of *E. gigantea* and *E. Dalrympleana*, gives way to a substantial area of well-grown *E. Dalrympleana* alone or with some *E. pauciflora* where the site is still favourable but not quite good enough for *E. gigantea*. At the upper limit *E. Dalrympleana* is replaced entirely by *E. pauciflora*. On adjoining, sharp, exposed ridges at the same elevation as *E. Dalrympleana* there is a stand of *E. dives* mixed with depauperate *E. Dalrympleana*. This at its upper limit and at approximately the same elevation as the upper limit of *E. Dalrympleana* joins the pervading *E. pauciflora* stand. The usual hybrids between *E. pauciflora* and *E. dives* occur at the stand junction between these two on rather poor sites which immediately adjoins the good site carrying large trees of *E. Dalrympleana*. The comparative failure of *E. Dalrympleana* to regenerate and the vigorous regeneration of *E. dives* and *E. pauciflora* have resulted in the replacement in regeneration under the now large fire-damaged trees of *E. Dalrympleana* of that species by a swarm of *E. dives* \times *E. pauciflora.* A new habitat has become available for this hybrid combination which was not available for it to colonize under virgin conditions, as it was fully occupied by *E. Dalrympleana.* As there is apparently some hybrid vigour or, at least in the early stages, rapid growth of the hybrids as compared with either parent, *E. dives* or *E. pauciflora,* the hybrid swarm has become the most biologically effective population to occupy this area.

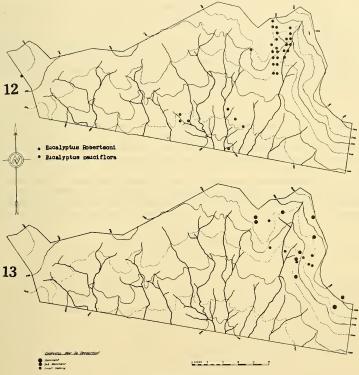
This kind of thing appears to be common, and a further good illustration with some variation is provided at Badja, some 20 miles north-east of Cooma. The arrangement of the species in the virgin condition in one section of this area is a little



Text-figures 10-11.

unusual in that there is a temperature inversion due to the physiography of the country, which results in E. radiata occurring towards the upper part of ridges, with E. pauciflora near the flat basin at the bottom, and E. Dalrympleana interposed in the intermediate zone between them. This arrangement is not unique and occurs in various similar areas in the highlands of the southern part of New South Wales. Here, where the stands have been subject to repeated fire since settlement, regeneration of E. Dalrympleana is very scarce. The old stands are opening up due to gradual destruction by burning, and regeneration of E. Dalrympleana, entering from above and

below into the original *E. Dalrympleana* stand. The regeneration under the *E. Dalrympleana* is a hybrid swarm between *E. radiata* and *E. pauciflora*, but the morphological characters indicating hybrid origin, which are well known from numerous progenies of this combination studied, if taken as an average at a series of points, show a definite gradation in the regeneration from almost pure *E. pauciflora* stock under the original *E. pauciflora* stands, through a series of graded intermediates to almost pure *E. radiata* regeneration under the *E. radiata* stand. In short, there is a hybrid swarm replacing the *E. Dalrympleana* and the swarm is graded according to the graded habitat conditions through the intermediate zone.



Text-figures 12-13.

SYSTEMATICS AND PLANT SOCIOLOGY.

The above considerations have a bearing on two other aspects of study dealing with *Eucolyptus*. Firstly, in considering the validity of any described species, it is fair to say, following the rule induced from the majority of established species, that if they are interbreeding they occupy distinctly different ecological habitats, any new forms being studied should be considered only as species or sub-species if they represent a population which occurs in a zone ecologically distinct from that occupied by related interbreeding species. If this criterion is applied to *Eucalyptus* species as at present described, the classification of the genus is at once somewhat simplified and a number of forms described as species can be properly placed in perspective in relation to the remainder. In the systematic revision of the genus which must be made at some time in the future, this criterion must be prominent in delimiting species.

In the field of plant sociology most workers describe forest types—or, as they are now generally called, "associations"—as proposed by Beadle and Costin (1952), in communities dominated by *Eucalyptus* species and they characterize them by the combination of dominant *Eucalyptus* species present. From the above study it is apparent that *Eucalyptus* communities fall into three distinct kinds:

1. The extensive (or ecologically unique) stable communities having dominants of combinations of two or more non-interbreeding species of *Eucalyptus* which might be called the *primary associations*.

2. Those which are of a limited extent and are unstable and occur only in a mixed zone at the junction between the two main species areas, and may therefore properly be described as *ecotones*.

3. Those resulting from combinations produced by disturbance following settlement which might be described as *secondary associations*, which are unstable in the absence of continued interference by man, and which generally (though it is not commonly recognized) contain trees which are members of hybrid swarms and are certainly not as genetically circumscribed as the species characteristic of virgin stands.

SUMMARY.

There is evidence that interbreeding *Eucalyptus* species occupy distinctly different ecological situations and that pairs of species which grow together in virgin conditions over substantial areas are reproductively isolated. Evidence is produced to show that hybrids occurred before settlement at the junction of two species-areas, and that this hybrid zone is probably the main source of hybrid swarms which have become prominent following settlement.

It is considered that the spread of hybrid swarms has been a direct result of settlement due to the major upset in balance of the plant communities by firing and clearing. The impact of these facts on *Eucalyptus* systematics and plant sociology is indicated.

References.

ANDERSON, E., 1949.—Introgressive Hybridisation. New York. BEADLE, N. C. W., and Costin, A. B., 1952.—Proc. Linn. Soc. N.S.W., 77:61-82.

ON AUSTRALIAN HELODIDAE (COLEOPTERA). I. DESCRIPTION OF NEW GENERA AND SPECIES.

By J. W. T. Armstrong.

(Thirteen Text-figures.)

[Read 29th April, 1953.]

Synopsis.

Three genera and fourteen species are described as new. Elodes ollifit Blackh., montivagons Blackh, variegata Cart., atkinsoni (Waterh.), cincta Blackh. and costellifera Cart., are found to have characters incompatible with that genus and are transferred to a new one, *Pseudo*microcara, to which eleven new species are added. *Elodes tigrina* is considered a synonym of variegata Cart. A key is given to the species. One new species is placed in *Macrocyphon* Pic, thus adding this genus to the Australian fauna. Additional generic characters are given. *Elodes australis* (Er.) cannot remain in that genus and is transferred to a new one, *Hetrocyphon*, to which a new species is added. The position of *Macrodascillus* Cart. is commented on and *Elodes scalaris* Lea transferred to it. One new species is placed in *Penceronatus*, n. gen. The shape of the mesosternal cavity is noted as a very useful taxonomic character, especially in *Cyphon*.

INTRODUCTION.

The author has been studying this family for a number of years and had much of the available Australian material before him. He has, also, representatives of most of the older described exotic genera of the Helodinae, and it soon became evident that many Australian species were misplaced in them. (*Elodes* does not occur in the Australian fauna.) It was therefore necessary to erect new genera for their reception. The shape of the mesosternal cavity has been found very useful in distinguishing species especially in *Cyphon* which will be dealt with in a later paper. In measuring the length of the insects the head has been excluded, as its position makes a material difference. The microscope used in preparing the figures reverses the images.

PSEUDOMICROCARA, n. gen. Helodinae.

Genotype, Pseudomicrocara orientalis, n. sp.

Form rather elongate, subdepressed, facies of Microcara.

Head covered by prothorax when withdrawn, with quite definite antennal fossae beneath eyes, front lightly convex, produced in a short muzzle. Eyes moderately prominent. Mandibles simple, wide, sharply pointed, but not long, very slender nor strongly overlapping. Antennae filiform, slender, about half length of body, second joint small, moniliform, third variable, remainder usually becoming progressively narrower. Maxillary palpi moderately slender, terminal joint a little shorter than penultimate. Labial palpi: terminal joint subcylindrical, slender, arising at an angle from end of penultimate. Labrum with apex broadly curved, tending to be constricted at base, separated from frons by a rather wide membranous area.

Prothorax about one-third narrower than elytra, semicircular in outline, sides and apex explanate, the latter extending a little over head, base bisinuate, anterior angles merged in general outline. Elytra usually about four times as long as prothorax. Legs of moderate length, moderately slender. Hind tarsi not bicarinate above, first joint long, second about half length of first, third about half that of second, fourth bilobed. Prosternum very narrow before coxae, prosternal process more or less diamond shaped, extending to about half-way between coxae but not nearly level with them. Mesosternum emarginate to receive prosternal process. Metasternum not produced forward between middle coxae. Fore and middle coxae narrowly separated, hind coxae contiguous, the latter transverse.

Distinguishing Characters.-This genus is separated from Microcara Thoms. and Elodes Latr. by the terminal joint of the labial palpi arising from the end of the penultimate, and from the latter also by the hind tarsi not being flat and bicarinate above and the second joint not overlapping and obscuring part of the third, etc. From *Macrohelodes* Blackb, it differs in being pubescent, in the metasternum not being produced forward between the middle coxae, and in many other respects. *Peneveronalus*, n. gen., has toothed mandibles, different palpi and a very differently shaped metasternum, etc. Typical species of *Cyphon* have a very different prothorax, the 4-11th antennal joints shorter in comparison with their width, and the mandibles distinctly toothed.

Discussion.

Pseudomicrocara orientalis, n. sp., has been chosen as the genotype as it is typical and appears to be the commonest species on the mainland. Six described species are transferred from the palaearctic and North American genus Elodes Latr., which is a well-characterized genus having the terminal joint of the labial palpi arising from the side of the penultimate and the hind tarsi bicarinate above with the second joint overlapping and concealing part of the third. This genus and Microcara also differ from Elodes conspicuously in the mesocoxae being transverse and narrowly separated, not elongate and contiguous, and in the hind coxae being much less strongly oblique from the transverse. It is noticed that in Microcara testacea L. the lateral prolongation of the posterior coxal plate deviates from the posterior margin of the metasternum.

The six species transferred are *Helodes atkinsoni* (Waterh.), *H. ollifi* Blackb., *H. cincta* Blackb., *H. montivagans* Blackb., *Elodes variegata* Cart. (= *tigrina* Cart.), and *E. costellifera* Cart. Eleven species are now described as new, making a total of seventeen.

Key to the species of Pseudomicrocara.

1 - 32.	Apex of the pronotum rounded, prosternal process more or less diamond shaped,
	intervals between elytral costae, when these are present, not convex.
2-3.	Third antennal joint about as long as 4th ollifi (Blackb.).
3-2.	Third antennal joint distinctly shorter than 4th.
4-5.	Pronotum testaceous, elytra black montivagans (Blackb.).
5-4.	Not so.
6 - 11.	Upper surface having a distinctly mottled or spotted appearance.
7-8.	Explanate pronotal margins reflexed, abdominal segments spotted (2-4-4-4-2) with
	black maculiventris, n. sp.
8-7.	Not so.
9 - 10.	Wider, larger, 6-9 mm variegata (Cart.) (= tigrina (Cart.)).
10- 9.	Narower, smaller, 3·25-4 mm picta, n. sp.
11- 6.	Upper surface not having a mottled or spotted appearance.
12 - 17.	Without trace of costae on elytra.
13 - 14.	Elytral punctures very fine atkinsoni (Waterh.).
14 - 13.	Elytral punctures rather coarse, at least on the disc.
15 - 16.	Elytral punctures uneven in size and distribution, size larger dixoni, n. sp.
16 - 15.	Elytral punctures coarse and even, size smaller infuscata, n. sp.
17-12.	At least three costae discernible on each elytron.
18-23.	Size smaller, less than 4.5 mm.
19-20.	Pronotum usually dark with pale lateral and apical margins, form elongate ovate
	variabilis, n. sp.
20 - 19.	Colour of upper surface uniform, form elongate sub-parallel.
21 - 22.	Pronotum less convex, subobsoletely punctate minor, n. sp.
22-21.	Pronotum more convex, finely but visibly punctate elongata, n. sp.
23 - 18.	Size larger, more than 4.5 mm.
24 - 25.	Mesosternal cavity twice as long as wide (length of insect 8 mm.) spencei, n. sp.
25 - 24.	Mesosternal cavity not longer than wide (smaller).
26-27.	Rather wider, red with centre of pronotum near base and disc of each elytron infuscated
	cincta (Blackb.).
27 - 26.	Narrower, colour of pronotum and elytra uniform.
28 - 29.	Elytra more elongate by comparison with pronotum, mesosternal cavity as wide as
	longelstoni, n. sp.
29 - 28,	Elytra less elongate by comparison with pronotum, mesosternal cavity transverse.
30-31.	Elytral punctures fine, eyes more prominent orientalis, n. sp.
31-30.	Elytral punctures rather coarse, eyes less prominent occidentalis, n. sp.
32 - 1.	Apex of pronotum subtruncate, prosternal process acuminate, elytral intervals between

costae convex costellifera (Cart.).

This key should be used with caution and as a guide to the descriptions, as there are probably still very similar species undescribed. It does not attempt to place the species in their natural order. They may, however, be provisionally grouped as follows: A—cincta, spencei, olliffi, orientalis, occidentalis, elstoni, minor, elongata, picta,

A.—cincia, spencer, only, orientatis, occidentatis, etsioni, minor, elongata, picta, variabilis, montivagans.

B.—atkinsoni, dixoni, infuscata.

C.—variegata.

D.—maculiventris.

E.—costellifera.

D. and E. are aberrant.

PSEUDOMICROCARA MONTIVAGANS (Blackb.).

Blackburn, T., 1892, Proc. LINN. Soc. N.S.W., vi: 519 (Helodes).

Type in British Muesum.

Type locality .--- Victoria, alpine district.

Synonym: Helodes montivagans Blackburn, loc. cit.

Note.—This species must also be removed from *Elodes* for the reasons given under *P. cincta* (Blackb.). It is at once distinguished from all other species assigned to this genus by the contrast between the testaceous prothorax and the black elytra. On nearly all the specimens before me the scutellum is black and on the majority the head, with the exception of the mouth parts, also is black. The infuscation of the pronotum mentioned in the original description is due to the head showing through from beneath. This species has a very close superficial resemblance to the American *Cyphon collaris* Guer.

Distribution.—Victoria: Alpine district (Blackburn Coll.), Heathmont (Ringwood) (Pottinger and Dixon), Bayswater (Dixon); South Australia: Murray River, Myponga, Mt. Lofty Rn. (Elston); N.S.W.: Sydney (Spence), Illawarra, National Park (Bryant), Wallace Lake (Carter), Dorrigo (Heron), George's R. (Davidson), Orange (Armstrong); Western Australia: King George's Sound (Macleay Museum). Any specimens dated were taken either in October or November.

PSEUDOMICROCARA VARIEGATA (Cart.).

Carter, H. J., 1935, PROC. LINN. Soc. N.S.W., 1x: 192 (Elodes).

Types in Coll. F. E. Wilson.

Type locality.--Warburton, Victoria.

Synonyms: Elodes variegata Cart., loc. cit.; Elodes tigrina Cart., loc. cit., 193, n. syn. Nore.—Mr. F. E. Wilson's paratype of *P. variegata* is before me, also a specimen taken by Dr. Nicholson at the same time as the types of *E. tigrina* which I believe to be this species and which is identical with the former. The only point at variance with the description is that the third antennal joint is much shorter than the following. Unfortunately the types of *E. tigrina* which should have been in the Macleay Museum seem to have been lost. In addition to the longitudinally carinate terminal abdominal segment in one sex $(? \ Q)$ the penultimate has a pronounced transverse brush of hairs. The original description omits to note two foveate depressions between the eyes. The head and pronotum are rugosely punctate, the antennae become progressively a little more slender in the female, the elytra are proportionately longer.

Distribution.—Victoria: Warburton, Millgrove, Belgrave (F.E.W.); N.S.W.: Dorrigo (Heron), Kosciusko (Nicholson), Narrabeen (Musgrave); Tasmania.

PSEUDOMICROCARA COSTELLIFERA (Cart.). Fig. 9.

Carter, H. J., 1935, PROC. LINN. Soc. N.S.W., 1x: 192 (Elodes).

Type in Coll. F. E. Wilson.

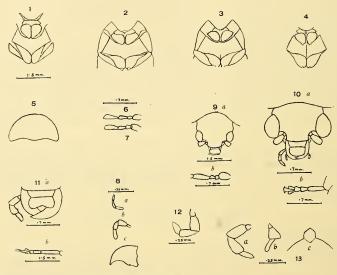
Type locality .-- Warburton, Victoria.

Synonyms: Carter, loc. cit., Elodes costellifera.

NOTE.—Types examined. This species also has labial palpi simple etc., and therefore cannot remain in *Elodes*. It is here placed in *Pseudomicrocara* with considerable hesitation pending more material for examination, as it is at least aberrant in its acuminate prosternal process and subtruncate pronotum. PSEUDOMICROCARA CINCTA (Blackb.).

Blackburn, T., 1892, Proc. LINN. Soc. N.S.W., vi: p. 518 (Helodes cinctus). Type in British Museum. Type locality.—Victoria, alpine district. Symonym: Helodes cinctus Blackburn, loc. cit.

NOTES: This species has the third joint of the labial palpi arising from the end of the second, which excludes it from the genus *Microcara* as well as from *Elodes*. The hind tarsi are not bicarinate above, nor is the third joint in great part concealed by the prolongation of the upper edge of the second, as is the case in the latter genus.



Text-figures 1-13.

1-4. Meso-metasternal regions of (1) Elodes minuta (L.), (2) Microcara testacea (L.), (3) Pseudomicrocara olliffi (Blackb.), and (4) Heterocyphon australis (Er.), drawn to same scale for comparison.

5. Pseudomicrocara orientalis, n. sp. Pronotum to same scale.

6. P. elstoni, n. sp. Antenna, first four joints.

7. P. orientalis, n. sp. Antenna, first four joints.

8. P. variabilis, n. sp. a, Labial palpus; b, maxillary palpus; c, mandible.

9. P. costellifera (Cart.). a, Head; b, antenna, first four joints.

10. P. orientalis, n. sp. a, Head; b, hind tarsus.

11. Macrodascillus denticornis Cart. a, Labrum, etc.; b, hind tarsus. (From type.)

12. Heterocyphon australis (Er.). Maxillary palpus.

13. Peneveronatus australis. n. sp. a, Maxillary palpus; b, labial palpus; c, mesosternal cavity.

A broad species, rather less than twice as long as wide, and very constant in colour which in combination renders it easily distinguishable from the other species placed in this genus.

Antennae: Second and third joints very small. Mesosternal cavity almost as long as wide, rounded at apex.

Distribution.--Victoria: Alpine district; New South Wales: Mt. Irvine, Acacia Plateau, Comboyne (Armstrong), Dorrigo (Heron).